Potential salinity limitations on nitrogen fixation in sediments from Mono Lake, California

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Abstract. Mono Lake is a hypersaline alkaline lake in the high altitude Great Basin desert of eastern California. Algal productivity of the lake is nitrogen-limited, and a contributing source is derived from benthic nitrogen fixation. Lake level and salinity have fluctuated with natural climatic variations but have also been affected by the diversion of tributary streams. This research examines the influence of varied salinity and lake level on the potential for benthic nitrogen fixation in Mono Lake. A sediment-surface microbial mat community was exposed directly, and in acclimated cultures, to a range of Mono Lake salinities under anaerobic incubations and the activity of nitrogenase assayed by acetylene reduction. Activity was stimulated in light, but also occurred in darkness. Over an experimental salinity range from 50 to 150 $g L^{-1}$ TDS, nitrogenase activity was reduced by 90 per cent, with the activity persisting at the highest salinity being attributable to dark fixation alone. Between a salinity of 50 $g L^{-1}$, occurring in Mono Lake over 50 years ago, and 100 $g L^{-1}$, nitrogenase activity was reduced by nearly half. Changes in the area of the littoral zone at varied lake levels also affect the total amount of potential benthic nitrogen fixation in the lake. An accounting of yearly inputs of nitrogen to Mono Lake suggests N_2-fixation could contribute as much as 76–81 percent of the total. Inhibition of nitrogen fixation rates by increased salinity could limit the long-term nutrient supply and benthic primary productivity of this ecosystem.

Key words: cyanobacteria, lake management, Mono Lake, nitrogen fixation, salinity, saline lakes

Introduction

Nitrogen fixation can play a significant role in the productivity of aquatic ecosystems, especially in nitrogen-deficient habitats (Horne and Goldman, 1972; Howarth et al., 1988). The process has been shown to be especially active in shallow waters within anoxic sediment zones rich in organic matter (Paerl and Carlton, 1988). While the dynamics of nitrogen fixation have been described in relation to the organisms responsible, physiological requirements, and environmental constraints in freshwater and marine ecosystems

(Paerl, 1990), few studies have been conducted in inland saline waters (Javor, 1989). Saline lakes often cover extensive shallow areas of anaerobic sediments containing detrital organic matter and so would appear to be suitable habitats for N_2-fixation. Though both benthic and planktonic nitrogen fixation have been reported in saline lakes (e.g. Potts, 1980; Horne and Galat, 1985), little is known of the influence of varied environmental salinity or chemical composition on N_2 fixation in these heterogeneous habitats.

Closed-basin inland salt lakes may exhibit rapid and frequent changes in elevation, volume and solute concentration, so the effect of salinity on nitrogen fixation is an essential consideration to the nitrogen budget and dynamics of such ecosystems. Mono Lake is an alkaline salt lake located in east-central California. Over the past 50 years the salinity of the lake has varied in the range of 50–100 g L^{-1} TDS due to stream diversions and drought, and contains high concentrations of carbonates, chloride, and sulfate salts of sodium at a pH near 10 (Herbst, 1988). The lake is currently meromictic with a chemocline near 15 m depth. At the 1997 surface elevation of 6380 ft (1944.6 m) the lake has a mean depth of 25.9 m, maximum depth of 47.2 m, and an area of about 180 km² (of which 60 km² covers a shallow water littoral zone 10 m deep). Benthic microbial mats composed mostly of diatoms and cyanobacteria grow on littoral deposits of sand and organic matter and on calcareous tufa rock formations.

Nitrogen fixation has been reported in Mono Lake sediments in association with decomposing aggregates of the filamentous green alga *Ctenocladus circinnatus* (Oremland, 1990). Sediment-surface anaerobic bacteria and non-heterocystous blue-green algae (*Oscillatoria* spp.) have been implicated as the primary organisms responsible for fixing nitrogen (Oremland, 1990). *Oscillatoria* is widely distributed over the benthic environment of Mono Lake, and occurs not only along with *Ctenocladus* aggregates, but as an integral part of microbial mats on both rock and organic sediment deposits. No planktonic nitrogen fixation has been detected.

Growth of planktonic and benthic algae in Mono Lake has been shown through enrichment cultures to be nitrogen-limited (Herbst and Bradley, 1989; Jellison, 1992). The cycling of nitrogen through bacterial remineralization of decomposing matter on the lake bottom, and mixing of regenerated ammonia into surface waters, is an important process in the annual renewal of nutrients for primary production (Jellison et al., 1993). Losses of nitrogen from the system are likely to occur through the volatilization of ammonia gas at the lake surface, and sediment burial of that fraction of nitrogen compounds that are refractory to remineralization. The purpose of the present study was to compare potential changes in nitrogen fixation due to varied salinity,

and the relative magnitude of different sources of nitrogen input to Mono Lake.

Between 1941 and 1988, the major tributary streams to Mono Lake were diverted to the city of Los Angeles via the Owens Valley aqueduct. The reduced inflow of water to this hydrologically closed desert basin caused the lake to evaporate to half its former volume and twice the salt concentration present before diversion. Recent resumption of stream flows ordered by the California State Water Resources Control Board are expected to raise the lake to a stable elevation about 6 m above the historic low level in 1982 of 6372 ft (1942.2 m). Assessment of the ecological effects of changing salinity and lake level provide information useful to the design of water management in the Mono Basin. The objective of the present study was to estimate potential changes in nitrogen fixation activity of Mono Lake sediments as a function of changes in salinity and benthic littoral area due to lake level fluctuation. Experimental salinities covered a range of environmental conditions above and below the present chemical concentration. Studies of nitrogen sources and sinks for Mono Lake (Jellison et al., 1993) indicated a disequilibrium in nitrogen fluxes, with losses in excess of inputs. The work reported here also addresses the potential role of nitrogen fixation in accounting for nitrogen budget deficits.

Materials and methods

Sediment-surface microbial mats (upper 10 mm) were collected from littoral margins on the west shore of Mono Lake (the "Old Marina") at a depth of 10 to 20 cm using a suction siphon. Insect larvae were sieved out, and the remaining sediments homogenized by repeated flushing from a 10 mL syringe. After allowing the sediments to settle, supernatant water was drawn off and 2.5 mL aliquots of the sediment slurry added to 20 mL of each treatment salinity in flasks of 58 mL total volume. Five salinity levels were prepared (50, 75, 100, 125, and 150 g L^{-1} total dissolved solids) using natural lake water. Salinities below 100 g L^{-1} (near the salinity at the time of this study), were prepared by dilution with distilled water and salinities above 100 g L^{-1} were prepared by evaporation in shallow pans. Treatment salinities were adjusted by mixing, to achieve specific gravities corresponding to the desired salinity levels.

In the first experiment, using sediments transferred directly from field collections, duplicate flasks were incubated in the light (15 μEinsteins m^{-2} s^{-1}), and one flask was kept dark by wrapping it in aluminum foil. A subsample of the sediment slurry was also autoclaved to sterilize the inoculum as an experimental control (2.5 mL sterile sediment + 20 mL treatment salinity). Sediments were immersed in each salinity treatment flask for 12 hours at

20 °C prior to starting experiments. Flasks were stoppered with serum caps, flushed with N_2 for 5 minutes, and a volume of acetylene gas equal to 15 per cent of the flask airspace (enzyme saturating concentration) introduced with a syringe and needle. Acetylene was generated by mixing CaC_2 with water. After 15 minutes equilibration on a shaker table (50 rpm), gas samples were withdrawn through the serum cap (0.25 mL), and analyzed along with standards by flame ionization gas chromatography to establish initial levels of ethylene (using the method of Hardy et al., 1968). Gas samples were subsequently removed after 1, 3, and 17 hours to measure nitrogenase activity.

In a second experiment, Mono Lake sediments were acclimated in cultures over the same range of salinities for one month and used in nitrogenase assays. This provided an opportunity for long-term physiological acclimation, differential growth, or changes in microbial species composition and dominance to occur. Culture flasks contained 50 mL of homogenized sediment in 200 mL of the unenriched treatment salinity. During the culture period, anaerobic microzones in the layered microbial mat developed (indicated by presence of a pink-red lower layer of purple sulfur bacteria), with less growth apparent in treatments at higher salinities. Nitrogenase activity assays were initiated in 58 mL capacity flasks containing 25 mL of homogenized culture slurry, using six replicates and one heat-killed control per treatment salinity. Sediment subsamples were also preserved for later drying and weighing. Flasks were kept in the light (light levels as above) under nitrogen over a 48 hours assay period. After determining initial ethylene levels, gas samples were withdrawn from replicates at intervals over the assay period. This produced a time course for nitrogenase activities that was analyzed by comparison of regression lines fit to quadratic functions and tested for overall differences by ANOVA and post-hoc multiple comparison tests between treatments (Fisher's least significant difference test).

To develop a simple model of lakewide benthic nitrogen fixation in relation to changing lake level and salinity it was also necessary to account for changes in benthic littoral area over which fixation could occur. Littoral area to a depth of 10 meters (within the epilimnion and zone of active benthic algal production) was determined from tables of lake surface area at different lake levels (JSA, 1993). Potential changes in benthic N-fixation at different lake levels were calculated as the product of littoral lake area and salinity-dependent N-fixation rate per area (using nitrogenase rates determined from direct-transferred field-collected sediments).

An estimate of nitrogen inputs to Mono Lake from stream flow and precipitation were derived from Jellison et al. (1993). Potential allochthonous input of nitrogen from vegetation was estimated for windblown tumbleweed from

Table 1. Nitrogenase activity in Mono Lake sediments exposed to varied salinities of Mono Lake water (direct transfer of field-collected sediments for this bioassay). Rates calculated for period between 4–20 hours of exposure (after initial lag period) in a nitrogen atmosphere containing 15 per cent acetylene. Data show rates of ethylene production (nmoles mL sediment^{-1} hour^{-1}) at each salinity in light-exposed duplicate flasks (L1 & L2) and in a single darkened flask (D)

	Treatment Salinity (g L^{-1} TDS)				
	50	75	100	125	150
L1	27.64	22.25	13.85	11.28	3.44
L2	24.90	23.76	14.06	6.06	2.42
D	10.61	6.01	4.52	7.24	3.12

surveys of *Salsola kali* cover and N content (Burch et al., 1977; Galat, 1986), and due to inundation of terrestrial vegetation by rising lake levels from plant community surveys (JSA, 1993).

Results

Nitrogenase activity was inhibited by increased salinity (Table 1), and most or all of the activity remaining in the higher salinity treatments was attributable to dark anaerobic fixation. Activity in light flasks was presumed to include both light-stimulated fixation and that fraction due to dark fixation. Control flasks possessed no activity and showed no differences between salinity levels. Nitrogenase activity was reduced by almost half between salinity treatments of 50 and 100 g L^{-1} (means of 26.3 vs 14.0 nmoles ethylene mL sediment^{-1} hr^{-1}, and by nearly 90 per cent between 50 and 150 g L^{-1} (to 2.9 nmoles mL^{-1} hr^{-1}). Over the lower salinity range, from 50 to 100 g L^{-1}, dark fixation accounts for 25 to 40 per cent of the total activity. Sediments contained several species of *Oscillatoria*, diatoms (Kociolek and Herbst, 1992), *Ctenocladus*, and bacteria including *Ectothiorhodospira*.

Nitrogenase activity in cultured sediments was also reduced with increased salinity above 75 g L^{-1} (Figure 1). No statistically significant differences were detected between 50 and 75 g L^{-1} (p > 0.10), but all other comparisons of regression lines were significantly different (p < 0.001). Rates over the 48 hour assay period were more variable at the lower salinities but averaged from 220 to 250 nmoles g^{-1} hr^{-1} at 50 and 75 g L^{-1} respectively, decreasing to 120 nmoles g^{-1} hr^{-1} at 100 g L^{-1}, to 70 nmoles g^{-1} hr^{-1} at
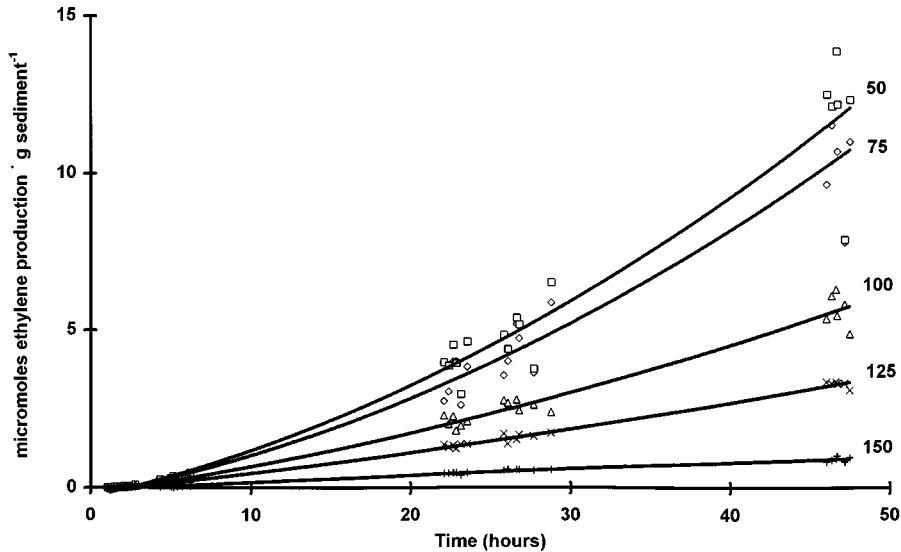
Figure 1. Nitrogenase activity in Mono Lake sediments acclimated under experimental treatment salinities for one month prior to activity assay. Same salinity range and assay methods as in Table 1 but using 6 light exposed replicate flasks per treatment and a time course of gas sample analyses from each. Lines fit to quadratic regressions.

125 g L^{-1}, and 20 nmoles g^{-1} hr^{-1} at 150 g L^{-1}, consistent with the relative differences observed in the experiment using unacclimated sediments.

The nitrogen fixation rates obtained in these laboratory studies may be related to areal rates in nature. One mL of sediment slurry (from the direct transfer bioassay, Table 1) is equal to 1 cm^2 of collected surface sediment to a depth of 1 cm. For a salinity of 100 g L^{-1} (approximate salinity at the time of these studies), the hourly rate of fixation is about 0.014 mole ethylene mL^{-1} hr^{-1}, which would occur on a daily average for 12 hours in the light and about one-third this rate in the dark (4 of 12 h + 12 daylight = 16 h). Converting to daily rates per m^2 gives an estimate of 2.24 mmoles m^{-2} day^{-1}. Using this estimate, and assuming a 4:1 conversion ratio of ethylene to nitrogen equivalents (Postgate, 1982), over 8 months of the year (240 days), to a depth of 10 meters in the benthic littoral zone (about 50 km^2 area at an elevation of 6375 ft or 1943.1 m), annual ammonia production from lakewide fixation for these conditions has the potential of generating 6.8 × 10^6 moles N (Figure 2). Using the same assumptions for cultured sediments examined in the present study (Figure 1), and 5 mL sediment per gram dry weight, the lakewide annual nitrogen fixation would be nearly 50 × 10^6 moles.
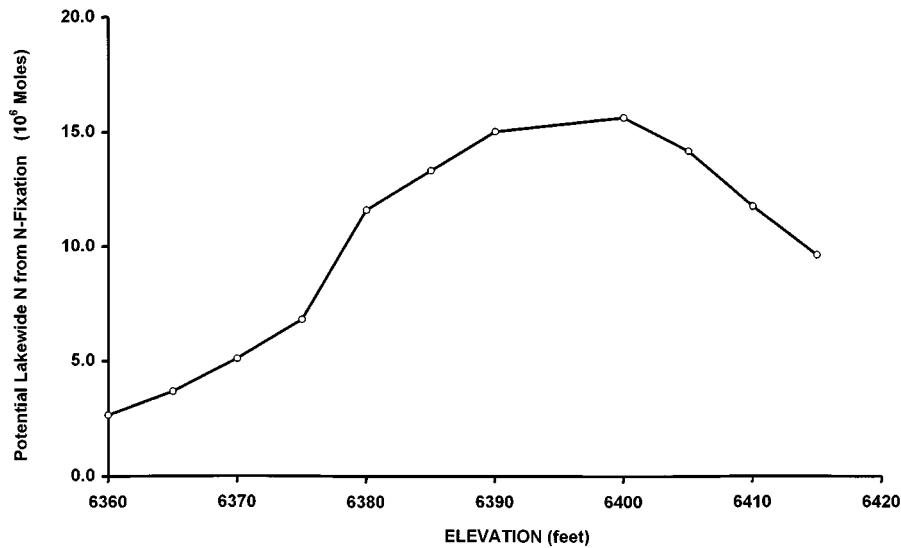
Figure 2. Potential annual lakewide benthic nitrogen fixation in Mono Lake at different lake surface elevations. Calculated as the product of salinity dependent nitrogen fixation rates (from Table 1 data) and benthic littoral area to a depth of 10 meters for the corresponding lake level (see text for example calculation).

A model of the interaction between salinity inhibition of nitrogen fixation and changes in the area of the littoral zone results in a calculated peak of potential benthic nitrogen fixation (Figure 2) between 6390 to 6400 feet elevation (1947.7 to 1951.2 meters). This model is intended to account only for the dependence of potential nitrogen fixation on salinity and littoral area for lake levels corresponding to the salinities tested.

An accounting of external sources of nitrogen in comparison to nitrogen fixation is given in Table 2 and is intended as an approximation of the range and relative magnitude of potential contributions from different nitrogen sources. Based on nitrogen content reported for Mono Basin stream and rain water (Jellison et al., 1993), annual inputs of combined nitrogen to Mono Lake can be estimated to average about 0.18 megamoles from streamflow, and about 0.30 from precipitation. Assuming the range of variation in stream discharge and precipitation is from approximately half to twice the average (Vorster, 1985), nitrogen inputs from these sources could range between about 0.09–0.36 and 0.15–0.60 megamoles, respectively.

Potential allochthonous input of nitrogen from windblown tumbleweed, *Salsola kali*, was estimated from the cover on the southeast lakeshore where this plant is most common and could be carried into the lake by prevailing southwesterly winds. Between elevations of 6390 and 6420 ft (1947.7 and

Table 2. Potential range of annual nitrogen inputs to Mono Lake from different sources (mol N $\times$ 10^6 yr^{-1}). Ranges derived from estimated nitrogen fixation at 6370 and 6400 ft lake elevation [based on nitrogenase rates in (1) directly exposed sediments in the present laboratory study and (2) *in situ* studies of Oremland (1990)], records of the range of variation in the volume of stream discharge and precipitation inputs to Mono Lake, and allochthonous vegetation inputs from estimates of plant area and cover (see text for further description)

Source	Range (10^6 moles N yr^{-1})
Nitrogen fixation (6370–6400 ft)	5.10–15.62 (1)
	0.80–2.45 (2)
Stream flow	0.09–0.36
Precipitation	0.15–0.60
Windblown *Salsola*	1.25–2.50
Inundated vegetation (transient)	0.10–0.20

1956.8 m), *Salsola* cover was estimated at 9.3 km^2. If plant densities were as high as found at Pyramid Lake by Galat (1986), and contained the same nitrogen content, this is equivalent to a yearly standing crop for this annual plant of 2.5 megamoles of nitrogen. Assuming, as did Galat et al. (1981), that half this amount might be transported into and remain in the lake, the potential annual contribution of nitrogen from tumbleweed could range between 1.25 to 2.5 megamoles. It should be noted that these are probably overestimates because plant cover is mixed on the SE shore of Mono Lake compared to the nearly pure tumbleweed stands at Pyramid Lake, and are only of recent historical importance since this exotic weed has been a significant vegetation element for little more than the past century.

During tributary stream diversions starting in 1941, Mono Lake declined from an elevation of 6417 ft (1955.9 m, ca. 50 g L^{-1}) to a historic low of 6372 ft (1942.2 m, ca. 100 g L^{-1}) in 1982. Exposed lake bottom was colonized by a variety of terrestrial plants during this period. Vegetation between 6375 and 6390 ft (1943.1–1947.7 m) will become inundated over the next 10–20 years as Mono Lake rises to meet the order of the State Water Resources Control Board. Nitrogen from this transient source of decomposing vegetation was estimated from the area covered by wetland, scrub, and dry meadow plant communities between these elevations around Mono Lake (JSA, 1993). Based on an area of 3.7 km^2 and assuming densities twice as high as for *Salsola*, and allochthonous organic matter with a C:N ratio of 45 (Hutchinson,

1957), gives an annual input in the range of 0.1 to 0.2 megamoles over the 10–20 years required for complete inundation.

Discussion

Nitrogen fixation in Mono Lake sediments is light-stimulated, indicating that the primary organism responsible is a phototroph, probably the nonhetero-cystous filamentous cyanobacterium *Oscillatoria*. Fixation occurring in the dark is likely due mainly to anaerobic bacteria. These comprise the two dia-zotrophic communities described by Oremland (1990). The studies reported here show that nitrogen fixation in sediments containing both these types of organisms is inhibited by increasing salinity, and that above 100 g L^{-1}, most or all of the activity is attributable to the anaerobic bacteria fraction. In addition, there is no evidence of acclimation or adaptation of nitrogen fixing organisms following a one month sediment culture period. Nitrogenase activity remains highest at 50 and 75 g L^{-1} and rates are reduced by about half with each 25 g L^{-1} step increase above these salinity levels.

Chemical limitations on nitrogen fixation in aquatic ecosystems have previously been attributed to deficiencies in phosphorus, iron, and molybdenum (Schindler, 1977; Howarth and Cole, 1985; Wurtsbaugh, 1988). Shortages of these elements reduce algal growth rates and the activity or synthesis of the nitrogenase enzyme. Results of the experiments reported here suggest that salinity may also be an important regulator of nitrogen fixation in saline lakes or estuaries. In osmotically conforming prokaryotic cells, nitrogenase activity may be limited by structural changes in the enzyme related to increasing intracellular ionic or osmotic strength that compromise molecular function. Alternatively, the mechanism of inhibition could be related to reduced pho-tosynthetic fixation of carbon needed to support nitrogenase activity. Studies with the marine cyanobacterium, *Rivularia atra*, have shown reduced nitro-gen fixation with increased salinity below seawater concentration (Reed and Stewart, 1983). Hypersaline seawater in lagoons in the Bahamas also inhib-ited nitrogen fixation in cyanobacterial microbial mats (Pinckney et al., 1995). Despite the view expressed by Paerl (1990) that similar physico-chemical constraints on N_2-fixation exist across salinities in both freshwater and marine environments, the present studies demonstrate that hypersalinity in athalassic environments can play a significant role in reducing N_2-fixation.

Previous estimates of nitrogenase activity in Mono Lake (Oremland, 1990 erratum) averaged 22 μmol C_2H_4 m^{-2} hr^{-1} compared to 140 μmol C_2H_4 m^{-2} hr^{-1} found in this study at comparable salinity. This higher figure may be attributable to the fact that the previous study examined only that fixation associated with detached and decomposing tufts of the benthic filamentous

green alga *Ctenocladus circinnatus* (tangled with *Oscillatoria* filaments). The earlier estimates may also be lower because these were measured *in situ* in domed chambers in shallow water where aerobic conditions predominate. Anoxic microzones favoring fixation are more likely to develop within a stable microbial mat growing on organic sediments.

The nitrogen fixation estimates derived from this study may be conservative because the microbial communities examined come from sediments of variable composition in shallow aerobic environments, and are exposed to heavy grazing by larvae of the alkali fly, *Ephydra hians* (Herbst, 1988), causing bioturbation of sediments which could disrupt anoxic microzones known to be conducive to N-fixation (Paerl, 1985). The sediment source used for these assays may therefore not be representative of habitats favoring the greatest nitrogen fixation activity. During SCUBA diving surveys of the distribution of the alkali fly, extensive benthic mats comprised mainly of *Oscillatoria* filaments were observed on sediments and rock surfaces to depths of at least 10 m in many littoral areas (Herbst and Bradley, 1993). The presence of reducing conditions at the boundary layer of these mats was indicated by black, sulfide-rich sediments immediately underlying the surface layer. The abundance of *Oscillatoria* and reduced larval grazing at these depths suggests that both the measurements reported here, and those of Oremland (1990 and erratum), may underestimate the nitrogen fixing potential of the benthic microbial community of Mono Lake. N_2-fixation at lower salinity levels in Mono Lake may be further underestimated here because they do not incorporate the possible shifts to nitrogen-fixing cyanobacteria that may inhabit the lake at lower salinity such as the *Nodularia spumigena* that are dominant in nearby low salinity lakes such as Walker and Pyramid Lakes in western Nevada.

Mono Lake benthic fixation is comparable to estuaries and other salt lakes. The daily rate of 2.24 mmoles ethylene m^{-2} found in this study is equivalent to 1.88 g N m^{-2} yr^{-1} (for 8 months per year), and is just above the upper range of values reported from organic-rich estuarine sediments (Howarth et al., 1988), but lower than rates found in near-shore sediments of Big Soda Lake, Nevada, an alkaline lake with a salinity of 26 g L^{-1} in the mixolimnion (Oremland, 1983). For an annual phytoplankton production in Mono Lake in the range of $3\text{-}13 \times 10^9$ mol C (Jellison and Melack, 1993) and $5\text{-}15 \times 10^6$ mol N fixation yr^{-1}, assuming a C:N ratio of 7 in live phytoplankton, benthic N_2-fixation can account for no more than 1–2 per cent of phytoplankton nitrogen requirements. The fraction of this nitrogen taken up by benthic algal mats would further reduce the small amount available to phytoplankton. This small percent of the N needs for primary production met by nitrogen fixation is typical of lakes, oceans and estuaries (Howarth et al., 1988).

Although nitrogen supply to planktonic production from benthic nitrogen fixation may prove to be insignificant on an annual basis, it could contribute as much as 76–81 per cent or as little as 33–40 per cent of total nitrogen input annually (depending on the rates used in Table 2), and compares with Pyramid Lake (81 per cent) and some other eutrophic lakes where activity reaches high rates (Howarth et al., 1988). N_2-fixation inputs estimated from this study are reasonable because they are expressed as a potential range using the lower rates obtained from unacclimated sediments, and fall between *in situ* rates found in Mono Lake and in Big Soda Lake. Only tumbleweed inputs were also estimated to have the potential to contribute a substantial portion of the annual nitrogen budget and these are probably overestimates. The large fraction of the nitrogen budget likely to be generated by fixation indicates this may be an important component of the long-term budget, and integral to supporting benthic algal productivity, especially during summer when dissolved ammonium concentrations are often low in surface waters (less than 1 μM, Jellison and Melack, 1993). That the amount of ammonium excreted by brine shrimp usually matches that required to meet phytoplankton demands during summer (Jellison, 1988) also suggests there is no excess nitrogen present during the growth season. Benthic nitrogen fixation may thus make little or no direct contribution to pelagic nutrient levels in summer, and littoral algae may receive little nitrogen from vertical mixing. Despite limited exchange indicated between littoral benthic and planktonic communities, a long-term nitrogen budget for Mono Lake is likely to depend on salinity-dependent couplings between benthic N_2-fixation, sediment fluxes, mixing, atmospheric losses, nitrification-denitrification, and requirements of benthic and planktonic algal growth.

Combining both salinity and littoral area limitations, and assuming no changes in the present N-fixing community, Figure 2 shows potential N supply from benthic fixation would be reduced both above and below a lake level range from 6390′ to 6400′ elevation (1947.7 to 1951.2 meters, around 75 g L^{-1} TDS). These data formed part of the evidentiary basis for the decision by the California State Water Resources Control Board ordering restoration of Mono Lake at or above 6390 ft elevation where potential benthic nitrogen fixation is maximized, among other ecological processes.

Studies of the nitrogen flux of Mono Lake (Jellison et al., 1993) indicate that current nitrogen input rates are insufficient to account for rates of ammonia flux out of the sediments. Sediment nitrogen is apparently being depleted more rapidly than it is being replaced. The current disequilibrium in nitrogen balance could in part be explained by greater inputs of fixed nitrogen and decomposable biomass from higher production under previous lower salinity conditions, with ammonia regeneration now drawing on these reserves of

nitrogen stored in sediments. The results reported here are consistent with this explanation, and indicate that the amount of nitrogen fixation has been higher under past moderate salinity conditions, and is likely to increase as future lake levels rise and salinity is reduced.

These results suggest that increased salinity, particularly from 50 to 100 g L^{-1}, may limit benthic nitrogen fixation inputs and constrain primary production in Mono Lake. Other studies have further shown that salinity reduces benthic algal growth rates and species diversity over the range from 50 to 100 g L^{-1} (Herbst and Bradley, 1989; Herbst and Castenholz, 1994; Herbst and Blinn, in press). As the dominant source of nitrogen in this lake and possibly other productive saline lakes, nitrogen fixation may control benthic primary production and long-term nutrient supplies only within the constraints imposed by salinity.

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